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ALLOMETRIC BODY/SCALE RELATIONSHIP IN ATLANTIC SALMON (*SALMO SALAR*) IN THE MARINE PHASE

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Although backcalculation methods using scale measurements have been applied to various fish species including the Atlantic salmon (*Salmo salar*), there have been few detailed studies on the relationship between body length and scale radius (henceforth referred to as the body/scale relationship) in this salmonid. The most complete study on the subject to date has been conducted by Lindroth (1963) who also mentions the investigations undertaken by Dahl (1910), Lindsay and Thompson (1932) and Kerr (1961).

Two definitions are needed for our discussion. When, in the lifetime of an organism, the proportion between two parts or a part and the entire

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organism remains constant, we speak of isometry. When, on the other hand, the proportion is not constant, we refer to allometry (Tessier, 1948; Bagenal and Tesch, 1978; Smith, 1980; Reiss, 1989). In this paper, the linear relationship will be called isometric, although this may not completely fit the definitions we have just given.

In backcalculating body length in adult salmon, it is customary to use a proportional relationship (Lindsay and Thompson, 1932; Lindroth, 1963, Anonymous, 1984), thereby assuming an isometric relationship. There are indications, however, that each stage (parr, smolt and adult) is characterized by its own specific body/scale relationship (Kerr, 1961; Lindroth, 1963). Since this study focuses on the body/scale relationship during the marine period, the relationship was established from a sampling of the entire range of sizes we intended to backcalculate (Carlander, 1981). In this way, it will subsequently be possible to backcalculate lengths during the marine phase and to compare 1-, 2-, and 3-sea-winter specimens (i.e., salmon that have spent 1, 2 and 3 winters, respectively, in the sea) as a function of age, length at the time of seaward migration and growth rates. This study is based on the body/scale relationship of the stock of Atlantic salmon in the St-Jean River, near Gaspé, Quebec.

Materials and Methods

The scales examined in this study were taken from smolts and adults in the St-Jean River (Gaspé), Quebec. The smolts were caught at the counting gate belonging to the Quebec Department of Recreation, Hunting and Fishing (Ministère du Loisir, de la Chasse et de la Pêche du Québec - MLCP). The

adults were caught either by MLCP employees in trapnets in the estuary from May to July or by sport fishermen.

The smolts were randomly collected at the gate every day for characterization of the seaward migrants (total body length, length to the fork in the tail, weight, sex, scale-determined age, etc.) (Ouellet and Turgeon, 1987; G. Ouellet and M. Turgeon, unpublished data). In the case of the adults caught in the trapnet, MLCP employees measured body length to the fork in the tail and removed a small number of key scales from each specimen (Lindroth, 1963). In the case of salmon caught by sport fishermen, the length to the fork in the tail was measured at the time the catch was registered, and a few scales were removed from the area between the end of the dorsal fin and the lateral line. These scales are referred to as standard scales. It has been shown in *Micropterus dolomieui* that there is no statistical difference in the body/scale relationships established from these two types of scales (Everhart, 1950, *in* Warner and Havey, 1961).

The scales and lengths used in this study were taken from MLCP collections by means of a systematic sampling approach (Frontier, 1983). In the case of the smolts, two subsamples were taken from each of the 1982, 1984 and 1985 samples (there were only 23 individuals in the 1983 sample). The first of the two subsamples (N = 103) was taken to establish the body/scale relationship. The second subsample (N = 546) contained only body length data and was intended for comparison with backcalculated lengths at smolting of adult specimens. Since the 1982 sampling contained only 182 individuals, the subsample size conferred a statistical weight equal to the three years

selected. In the case of the adults, the subsample (N = 338) was taken from the 1983 to 1986 collections and contained 98, 66, 102 and 72 scales and length measurements, respectively.

Smears of smolt scales were prepared on heat-sealed plastic slides. Adult scales were cleaned in soapy water and initially examined for suitability for this study. We selected symmetrical scales that had intact edges and the original cores but no spawning marks. According to an anonymous article published in 1984, the scale should measure less than 0.5 mm from the centre to the first circulus. We selected only scales in which the diameter of the core was less than 0.4 mm since there is evidence that in rivers with very cold water, such as the St-Jean River, the first annulus may be missing (Jensen and Johnson, 1982). Each of the selected scales was then mounted between a cover slip and glass slide.

The river and sea age was determined and marked on each slide in accordance with the usual notation system used for salmon (Anonymous, 1984). One of the mounted scales was then measured by means of an image analyzer (Optical Pattern Recognition System, Biosonics Inc.). For each annual mark (annulus), the medio-anterior radial was measured to the outer limit of the winter zone.

In order to determine whether the use of a single scale per individual could induce additional variability in the body/scale relationship, measurements were taken of a small number of scales from 29 adult specimens. It was found that the variance of scales was far greater between fish

specimens than within the same specimen (analysis of variance: df = 28.97; $F = 17.01$; $p < 0.0001$).

Backcalculation is a two-stage process. In the first stage, the body/scale relationship is statistically analysed for the purpose of deriving an equation which generally describes the length of the fish as a function of the scale. In the second stage, annulus measurements are converted into lengths by means of the parameters of the equation obtained in the first stage.

The first backcalculation stage raises some biostatistical problems. Since the body/scale relationship is not necessarily linear, a linear regression is unsuitable for the analysis in that it fails to provide a clear comparison of fits to data that have been transformed for the purpose of making the relationship linear (Bartlett et al., 1984).

Furthermore, it is assumed when fitting a linear regression by the method of least squares (predictive regression) that the dependent variable (in this case, the length) is responsible for any variability in the body/scale relationship, and this cannot be justified either biologically or statistically. Tessier (1948) and Ricker (1973, 1984) suggested using functional regressions to apportion variance between the two variables.

Lastly, Smale and Taylor (1987) have stated that the most accurate estimate of the parameters in the equation describing the body/scale relationship is achieved with mean radial values for the various length classes. With this approach, the scale-induced variance can be reduced and stabiliz

Bartlett et al. (1984) have suggested using covariance analysis for an objective study of the body/scale relationship since it provides a systematic basis for selecting the equation for backcalculating. This type of analysis, which has also been described by Snedecor and Cochran (1980), was used for the Atlantic salmon. A linear regression was applied to the set of data, then to each of the groups determined by the sea age of the fish at the time of capture and, lastly, to the mean length and scale radial values for each age group (barycentres). Variance of the body/scale relationship was thus apportioned according to its sources of origin. Each one was tested in the following order: the difference between the regression slopes of the groups indicated whether data transformation was needed. Deviation of the barycentres from a straight line indicated the degree of linearity of the relationship. The difference between the slopes of regression on the groups and the slope of regression on the barycentres established the extent to which variance was due to scale variability. Lastly, in the absence of any other significant source, the regression for the set of data indicated the strength of the link connecting body length and scale values. Since the variance of the regressions acted as a basis for the tests and was the same for functional or predictive regression (Ricker, 1973), the method seemed completely appropriate for this study.

In order to conform to the conditions for applying covariance analysis, we checked length and radial data for normality using a Kolgomorov-Smirnov test. On the basis of an equality of variance test (Hartley's F_{max}; Sokal and Rohlf, 1981), it was considered advisable to transform the data before undertaking analysis when smolts were included in the group. A log-log transformation was carried out for this purpose.

For the second backcalculation stage, it has been pointed out (Carlander (1981) and Gutreuter (1987)) that the most accurate conversion of scale radial values into lengths is achieved by the proportional method. The equation for conversion is:

$$(1)\quad L_1 = a + \frac{(L_c - a)}{R_t} R_1$$

where L_1 is the length at a given age, L_c is the length at the time of capture, R_t is the total scale radial value, R_1 is the radial value at the annulus being considered and *a* is the ordinate at the origin of the fitted linear regression. This is the Fraser-Lee equation. When parameter *a* is equal to zero, the Dahl-Lea backcalculation equation is used (Hile, 1970; Bagenal and Tesch, 1978; Bartlett et al., 1984).

Results

In order to test the generally held hypothesis that the relationship between body length and the scale is isometric, an analysis of covariance was carried out on the adult specimens only (untransformed data). Findings indicated that the hypothesis of an isometric relationship was completely justified (Table 1a; $F = 0.91$). The regression on the barycentres of the age groups was indeed linear ($p = 0.014$, $R^2 = 0.999$).

When data for the adults and smolts were combined, and variances were made homogeneous by means of log-log transformation (which amounts to testing the so-called allometric relationship, $Y = aX^b$), the hypothesis of an isometric relationship had to be rejected (Table 1b, $F = 76.03$). The hypothesis of an isometric relationship was no longer applicable between the

smolt and adult stages. Curvature of the body/scale relationship during the first winter at sea is the only way of explaining the slope of the relationship at the smolt and adult stages (Fig. 1).

Table 1. Analysis of covariance of the body/scale relationship in a) adults from the St-Jean River for the years from 1983 to 1986 and b) adults and smolts combined for the years from 1982 to 1986

Cause of Variation	Sum of Squares	df	Mean Square	F	p
	a) adults alone, 1983 to 1986				
Total					
Regression of total sample					
Differences in groups and barycentres					
Deviation of barycentres from the straight line					
Between slopes of the groups					
Residual					
	b) adults and smolts, 1982 to 1986				
Total					
Regression of total sample					
Differences in groups and barycentres					
Deviation of barycentres from the straight line					
Between slopes of the groups					
Residual					

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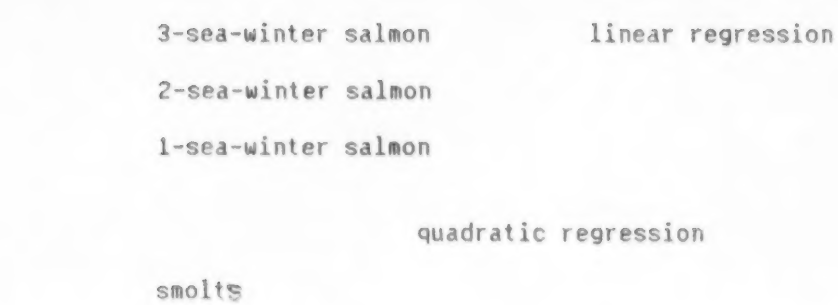

Fig. 1. Comparison of a linear regression with a quadratic regression for fit to length classes as functions of mean scale radial values for salmon in the St-Jean River for the years 1983 to 1986 ($Y = -3.74 + 20.72X$ for the linear form, $Y = -9.13 + 2.31\ X + 1.72X^2$ for the quadratic form; 3-cm intervals for the adults, 0.5-cm intervals for the smolts).

Table 2. Comparison of linear, quadratic, allometric and semi-logarithmic regressions for fit to length classes as functions of mean radial values for salmon in the St-Jean River for the years 1983 to 1986.

Model	df	Mean square	Estimate of parameters	Deviation from the mean
Linear				
Residuals				
Quadratic				
Residuals				
Allometric				
Residuals				
Semi-log				
Residuals				

(Replace the commas in the figures with periods - Translator)

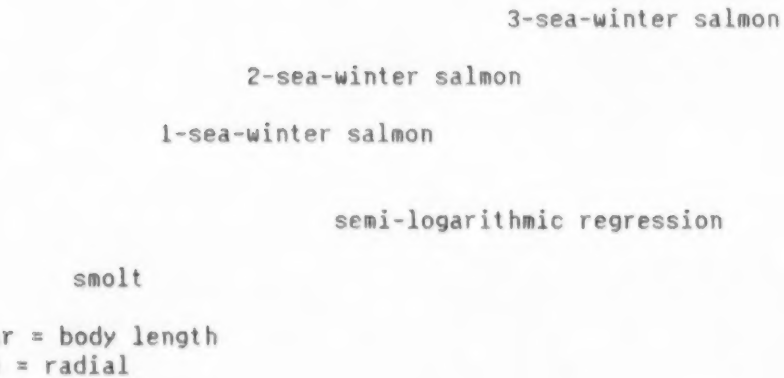

Fig. 2 Fit of a curvilinear regression, $Y = e^{2.15 + 0.57X}$, to length classes as functions of mean scale radial values for salmon in the St-Jean River for the years 1982 to 1986 (3-cm intervals for the adults and 0.5-cm intervals for the smolts).

Table 3. Comparison of lengths (cm) observed in smolts at the MLCP counting gate on the St-Jean River for the years 1982, 1984 and 1985 and lengths backcalculated from adult scales obtained in 1983 to 1986.

Statistics	Calculated	Observed
Number of cases		
Mean		
Mode		
Variance		
Minimum		
Maximum		
Skewness		

(Replace the commas in the figures with periods - Translator)

It therefore became necessary to fit a curve to combined adult-smolt data. Kerr (1961) suggested the use of a quadratic form for adults and parr together, but with this approach, 1-sea-winter salmon occur mostly to the right of the curve and the 3-sea-winter fish to the left (Fig. 1). Moreover, the same phenomenon occurs if a linear regression is used to backcalculate body length in smolts. The situation is essentially the same if the allometric equation generally suggested for similar cases is used (Tessier, 1948; Sokal and Rohlf, 1981; Conan and Comeau, 1986; Reiss, 1989).

Furthermore, results also indicate that the variability of the scales influences the overall regression on the group of adults considered alone (Table 1a; $F = 1\ 329.67$). The variability of the scales also influences the overall regression when smolts are included in the analysis after log-log transformation (Table 1b, $F = 2\ 136.74$). At this stage, therefore, computations should involve only the mean radial value for each length class, as has been suggested by Bagenal and Tesch (1978) and Smale and Taylor (1987), if scale-induced variance is to be reduced and stabilized. Analysis of covariance, however, can no longer be used.

The best fit is achieved with a semi-logarithmic relationship for the mean radial values for the various length classes (Table 2). The equation that best describes the body/scale relationship is therefore:

(2) $Y = e^{2.15 + 0.57X}$

($p < 0.01$, $R^2 = 0.988$). This equation conforms to the conclusions drawn from the covariance analysis of the total adult-smolt sample. The slope of the equation is similar to that of smolts in this length range and readily fits

the mean length and radial values for all the age groups. In addition, with this equation, there are just as many 1-sea-winter (or 3-sea-winter) salmon on one side of the curve as on the other (Fig. 2).

The equation permits satisfactory backcalculation of length in fish migrating to the sea by restoring equation 2 to a linear form and using the proportional method. Each individual is then considered to have its own specific body/scale relationship which, with growth, gradually deviates from that for the population as a whole, an hypothesis previously suggested by Bartlett et al. (1984) and Hile (1970). Thus, the hypothetical deviation of the individual scale value from the mean scale value in the relationship $Y = a + bX$ (logarithmic transformation of equation 2) is proportional to the logarithm of the length. Under the form of equation 2, individual deviations from the mean population value follow a curvilinear relationship similar to the population's body/scale relationship. We adjusted backcalculated lengths to be able to use a logarithmic equation (Sprugel, 1983).

Smolt lengths recorded at the counting gate were compared to backcalculated values obtained from same-stage adult scales (Table 3). The mean value for lengths that were backcalculated from adult scales was similar to the mean length of smolts at the MLCP counting gate ($t = 1.822$; $p = 0.07$). However, distribution was not the same (Kolmogorov-Smirnov test, $dN = 0.174$; $p < 0.0001$). With backcalculation, there were proportionately more smaller and larger migrating fish than were actually observed (Fig. 3). There are two possible interpretations for this distribution. If greater significance is given to mean values in comparing distributions, our findings suggest a higher

mortality rate among intermediate-size salmon during the marine phase. If, on the other hand, the mode is taken into account, flattening of the backcalculated distribution curve may be due to other statistical or biological factors that were not considered during the analysis. The greater spread to the right would, therefore, suggest an enhanced survival rate among larger individuals at the time of seaward migration.

Discussion

Comparing the findings of the covariance analysis of the data with or without the inclusion of the smolts clearly demonstrated that the body/scale relationship during the marine phase in Atlantic salmon was allometric. Including smolts in the group reduced the rectilinearity of the relationship fitted to the mean body length and radial values for each age group. Yet, the hypothesis of an isometric relationship generally put forward for the adults still seems to hold. As a result, our findings suggest curvature of the relationship during the first sea year (in the period between the smolt and 1-sea-winter stage), and this is demonstrable only with the inclusion of smolt scales.

Furthermore, the slope of the line fitted to the barycentres of age groups differs significantly from the slopes of lines fitted to each age group (the covariable used here is the sea age of the salmon). The variability of the scale, therefore, influences backcalculations based on a fitted regression on the entire sample. Backcalculation of fish sizes at the time of seaward migration from a linear regression on adult and smolt measurements, moreover, produces values that are either too high or too low.

The allometric equation generally used in such situations (Tessier, 1948; Smith, 1980; Sokal and Rohlf, 1981; Conan and Comeau, 1986; Reiss, 1989) permits equalization of the variances through the log-log transformation it implies, but it does not yield better results. By way of illustration, the exponent b in the allometric equation $Y = aX^b$ (tested in Table 1b) was equal to 1.02. In other words, the equation differed only very slightly from the line fitted to the untransformed data on adults and smolts. This is due to the fact that the allometric relationship is not designed to study trends among age groups (Reiss, 1989) and cannot be used to identify the problem related to variability of the scale. Furthermore, it must pass through the point of origin.

The best fit is achieved with a semi-logarithmic regression on length classes as functions of mean scale radial values (Table 2). The semi-logarithmic form conforms to mean length and radial values by age group (Fig. 2) and permits proper backcalculation of length at the time of seaward migration (Table 3).

It is evident, however, that while such a form permits calculation of smolt size, it will systematically overestimate parr size. This consequently means further curvature of the body/scale relationship between the parr and smolt stages. This has already been pointed out by Kerr (1961) and Lindroth (1963).

Backcalculated length distribution at the time of seaward migation suggests that intermediate size smolts suffer from a higher mortality rate

during their marine phase (Fig. 3). Another interpretation is that the greater spread to the right in the distribution curve, a phenomenon recorded also at the smolt stage, is reinforced by a higher survival rate among the larger smolts. There are documented cases of selective mortality among smolts. It has been demonstrated, although not necessarily accepted, that there may be a positive correlation between survival and smolt size (Chadwick, 1987; McCormick and Naiman, 1984). It has been reported (Ritter (1989), moreover, that individuals migrating at the beginning and at the end of the migration period are less apt to survive.

Fréquence = Incidence
Longueur = Length
Tailles observées = Observed lengths
Tailles rétrocalculées = Backcalculated lengths

Fig. 3. Histograms of relative incidence comparing lengths of seaward migrating smolts determined by retrocalculation using adult scales and by direct observation of migrating smolts in the St-Jean River (observed lengths: 1982, 1984 and 1985; backcalculated lengths: 1983, 1984, 1985 and 1986).

The use of a curvilinear relationship suggests that growth in salmon in their first sea year is overestimated by linear and quadratic equations. Because of the systematic bias introduced by these forms (the 1-sea-winter fish to the right of the curve and the 3-sea-year salmon to the left), the growth of 1-sea-year salmon is underestimated compared to that of the other adults during the first year in the sea. On the other hand, the growth of 3-sea-winter salmon is overestimated. This finding sheds new light the significant differences in the number of circuli in the annulus representing the first winter at sea that were recorded by Lear and Misra (1978) in the scales of 1-sea winter salmon, compared to 2-sea-winter salmon in certain Maritime stocks. This suggests that growth patterns are not the same in these two sea age groups.

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